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THE BOTANICAL REVIEW

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SEED GERMINATION PROBLEMS IN THE UMBELLIFERAE

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INTRODUCTION

An important problem often encountered in the culture of carrots, celery, parsley, parsnips and other economically important members of the Umbelliferae has been poor germination of seeds. Over 50 years ago Saunders (91) reported an average of only 43 per cent germination with carrot seed, no germination with celery seed, and Pieters (83) obtained germination of only 58 per cent with carrot and 53 per cent with parsley from "supposed reliable seedsmen". In 1907 Fraser, Gilmore and Clark (42) reported that as many as 80 seeds had to be sown for each carrot harvested. Tests by Brown and Goss (14, 15) and Oswald (81) during the first part of this century revealed that most of the carrot, celery, parsley and parsnip seed offered for sale did not meet the germination standards of that day. Work by later investigators has shown that poor germination is of common occurrence in the Umbelliferae and occurs despite the most diligent efforts taken by seed companies to produce high quality seed. Consequently the germination standards for the cultivated members of the Umbelliferae have been reduced and are considerably lower than for most other plants; only 55 per cent germination for carrots, celeriac and celery, and 60 per cent for parsley and parsnips is required under the Federal Seed Act (108).

Considerable research has been devoted to the factors responsible for the low percentage of germination encountered in the Umbelli-

[1] I would like to express my deep appreciation to Professor Harlan K. Pratt for his encouragement and assistance in the preparation of this manuscript, and to Professor James F. Harrington for advice and assistance in searching the literature.

ferae. Investigations have revealed the occurrence of three types of seed which show reduced or delayed germination: embryoless seeds, which are non-viable; seeds with rudimentary embryos, which may germinate after a period of storage; and seeds with a dormant embryo, which require particular temperature and light conditions for germination.

In the Umbelliferae the mature fruit is dry and splits into two parts, each of which contains one seed. The seeds, plus the adherent fruit wall, are universally termed "seed" by the trade. Though this terminology is not precise, particularly where the term "seed coat" is used, it is adopted here for simplicity.

EMBRYOLESS SEEDS

The most comprehensive study of one of the reasons for poor germination in the Umbelliferae is that by Flemion and her colleagues at the Boyce Thompson Institute for Plant Research. Examination of seeds of dill revealed that many did not contain an embryo (38). The seed coat and endosperm were apparently normal, but there was an empty cavity where the small embryo normally is embedded. Embryoless seeds were found in each of the 12 lots of fresh dill seed examined, and there was a clear relation between the number of embryoless seeds and the per cent germination in each lot. Four of the lots had many embryoless seeds, ranging from 39 to 62 per cent, and had very poor germination—24 to 54 per cent. The other lots had a relatively small number of embryoless seeds (7 to 14 per cent) and had very good germination (82 to 94 per cent).

Further investigations (32, 37) revealed that poor germination due to embryoless seeds is not limited to dill alone but is common in other members of the Umbelliferae as well. Seeds from representatives of 16 genera within the family were examined, and embryoless seeds were found in all but one. The number of embryoless seeds in the samples of cultivated members ranged from two per cent for coriander to 34 per cent for Florence fennel. Durfee (28), Mann and MacGillivray (73), and Munn and Heit (77) also reported that a large proportion of seeds of Umbelliferous crops are embryoless.

It may be supposed that seeds with good germination might be obtained by separating embryoless from normal seeds during clean-

ing, but it is impossible to achieve the separation mechanically because embryoless seeds weigh practically the same as normal seeds. The reason for this similarity is that the embryo constitutes but a very small part of the seed. It has been calculated by J. F. Harrington (unpub.) that the embryo makes up only about one per cent of the weight of a carrot seed; 100 soaked carrot seeds weighed 0.2356 gm., and 100 embryos removed from soaked seeds weighed but 0.0024 gm. The only feasible way of obtaining seed free of embryolessness is to contol the factor or factors responsible for the condition.

Flemion and her colleagues therefore began an investigation of the possible causes. Seed grown in Holland, Denmark, North Africa, Egypt, Norway and several areas in the United States were examined (32, 38). Embryoless seeds were detected in samples from each region, so the absence of embryos could not be attributed to a factor specific to certain areas of seed production. The year in which the seed was produced was also found to have no significant effect on embryolessness (37). A study of different varieties of carrot, celery and parsnip did not reveal any significant differences due to variety (37). Spacing of the plants does not affect the number of embryoless seeds (32) or the percentage germination (48) of the seed produced. No correlation was detected between seed size and the occurrence of embryoless seeds (32), and seed size has, in general, little effect on germination, although the smallest may show reduced germination (73, 100). The seed-yield of dill plants was not correlated with the amount of embryolessness (32).

In order to study possible genetic influence, two lots of dill seed were planted, one lot having few embryoless seeds, the other many (32). No significant difference was observed between seed produced by plants from the lot with eight per cent embryoless seeds and that produced by the plants from the lot with 38 per cent. This experiment, however, did not rule out the possibility that heredity influenced the development of embryoless seeds, because the seeds sown were a mixture of open-pollinated seed from many different plants. In corn it has been found that embryoless seeds may be caused by several recessive genes (25, 72, 90, 111), but there is no reason to believe that embryoless seeds in the Umbelliferae may be due to deleterious genes. Later tests, in which individual plants of dill and other members of the family were enclosed in separate

cages and self-pollinated by flies, resulted in the production of very few embryoless seeds, indicating that the parents were not heterozygous for genes such as those in corn (31, 35, 36).

Other possible factors were also studied (32), including climate, soil type and position of the seed on the plant. The climate was found to have no significant effect on the development of embryoless seeds, agreeing with Borthwick's finding that the temperature during the time of pollination does not affect germination (11). No correlation was discovered between embryolessness and seed production on soil types ranging from light sandy loam to heavy adobe. Various fertilizers were added to the soil and found to have no apparent effect on the amount of embryolessness (32) or the germination of the seed produced (11). Flemion did note that there was a tendency for seed produced later in the season to have a higher percentage of embryoless seeds than that of the earlier seed. For Beneš (10) and Borthwick (11, 13), seed produced on the first order of carrot umbels, which is the termination of the main axis and the earliest umbel on the plant to flower, germinated better than that of later order umbels, but Flemion (32) did not detect any correlation between the amount of embryolessness and the position of the seed on the plant.

None of the factors studied by Flemion et al. in their early reports (32, 37, 38) was found to be the cause of embryolessness, but several interesting observations were made. It was noted that embryolessness is a universal problem; it seems to occur among all members of the Umbelliferae and in all areas of the world. It was also noted that approximately 90 per cent of the time both seeds of the two-seeded schizocarp were similar in that both contained embryos or both were embryoless. In only ten per cent of the 66 pairs of seeds studied was one seed with and the other without an embryo. Another interesting finding was that embryolessness seemed to be correlated with the season of the year. One lot of dill seed produced eight per cent embryoless seeds in the early planting and 20 per cent in the later planting; another lot gave nine per cent embryoless in the early and 17 per cent in the later planting (32). The most significant observation was made in an experiment with greenhouse-grown dill plants which were caged so that flies might be enclosed to ensure pollination. These plants did not produce any embryoless seeds (32).

Flemion and her co-workers were finally successful in their quest for the cause of embryoless seeds in the Umbelliferae. They enclosed various insects, known to visit umbelliferous plants, inside insect-tight cages with dill plants (31, 35, 36). Flies were kept continuously in the cages for pollination. There was an average of less than one per cent embryoless seeds in the controls (caged, no insects other than flies) and in the cages with ants, fireflies, Japanese beetles, lace wings, ladybird beetles and syrphid flies. When the tarnished plant bug (*Lygus oblineatus* Say) was introduced, however, there was a range of 33 to 85 per cent embryoless seeds. Both nymphs and adults were found to destroy the embryo at almost any stage of development. Even when only one adult *Lygus* bug was enclosed for but 48 hours, as much as 18 per cent embryoless seed resulted.

These findings provide an explanation for the observations made in previous papers. The *Lygus* bug is widely distributed throughout the world, so it is not surprising that embryoless seeds were noted in samples from all sources. The increase in embryolessness as the season advances is in accordance with the natural buildup of the *Lygus* bug population during summer. The fact that both seeds of a pair are usually similar in both being either normal or embryoles can be explained by the tendency of the *Lygus* bugs to feed on both seeds of a given pair during one feeding period. The dill plants that were grown in insect-free cages did not produce any embryoless seeds because *Lygus* bugs were excluded.

Lygus bugs were enclosed with other members of the Umbelliferae, including carrot (both wild and cultivated), celery, coriander, fennel, goutweed, parsley and parsnip (35). The results of these experiments are in agreement with the findings with dill plants. Embryoless seeds were always produced when the tarnished plant bug was enclosed, ranging from 16 per cent (parsnip) to 100 per cent (parsley), while the controls—caged without *Lygus* bugs—had few or no embryoless seeds. Studies were also made with the striped cucumber beetle, the smartweed flea beetle and the stinkbug; these insects may cause some injury to dill and fennel seed but do not cause embryolessness.

By introducing *Lygus* bugs into caged dill plants in different stages of maturity it was found that the insects may cause reduced seed yield as well as embryolessness. Embryoless seeds were

produced when the *Lygus* bugs were introduced during the early stages of seed development, but when they were introduced during the flowering stage, there was also a large amount of flower destruction and consequently a reduction in seed yield (35). The study made by Handford (45) is evidence of the seriousness of this reduction in seed yield. A yield of 241 pounds of seed per acre was obtained in a carrot field when the *Lygus* bug was controlled by three applications of DDT dust. When the insect was not controlled, the yield was only 101 pounds per acre.

The *Lygus* bug has been found to injure the vegetative parts of umbelliferous plants as well as to cause embryoless seeds and reduced seed yields. Flemion and MacNear (33) enclosed *Lygus* bugs with dill and fennel plants prior to the flowering stage. The terminal growing points and tips of leaves were injured in this experiment, thereby bringing about reduction of growth. Injury to leaves of celery by *Lygus* feeding has been reported by Davis (24), Hill (53), Richardson (85) and Troop (106).

Embryoless seeds have been found to occur in plants of other families, including barley (46, 69), soft chess (2), corn (25, 72, 90, 111), *Datura* (89), rice (67), rye (69) and wheat (69, 70). In none of these plants, however, have the embryoless seeds been shown to be caused by *Lygus* bugs. Usually less than one per cent of the seeds of plants other than members of the Umbelliferae will be embryoless.

Although the *Lygus* bug has not been regarded as causing embryoless seeds except in the Umbelliferae, the insect is known to damage the seed crop of other plants. Injury is done to the flowers and young fruit of many crops, including alfalfa (17, 18, 94, 95), beans (8, 9, 92), cotton (74, 76, 103), guayule (3, 87) and sugar beets (27, 54, 55, 56, 57, 58).

Investigations have been conducted on the methods by which the *Lygus* bug produces such detrimental effects. Possible causes which have been studied are: *a*) transfer of a virus or of bacteria by the insect; *b*) physical injury by insertion of the insect's stylets into the plant tissue and removal of plant sap; *c*) chemical injury by a toxic substance in the saliva of the *Lygus* bug.

It appears unlikely that the insect serves as the vector of a pathogen, because the injury is limited to the site of feeding and is nontransmissible (65). Awati (6), Taylor (103) and others have noted that the *Lygus* bug withdraws and reinserts its stylets into

the same area of the host tissue repeatedly while feeding. This has been cited as evidence favoring the theory of mechanical injury (103), because repeated reinsertions in one area would lead to maceration of the tissue at that spot. Nevertheless it is not likely that the primary cause of the deleterious effects is merely mechanical injury to the tissue and removal of the plant sap during feeding. Other sucking insects seem to do similar physical damage but do not cause embryolessness or destruction of flowers and young fruit. Smith (93) attempted to cause mechanical injury to plant tissue artificially in a manner similar to that of the *Lygus* bug but was unable to duplicate the damage caused by the insect. On speculative grounds, Forbes (40) was one of the first workers to favor mechanical injury as the explanation. He criticized the theory that the injury was caused by injection of a toxic substance on the grounds that it could not be of selective advantage: " It is contrary to the order of nature that a habit of this sort should be acquired, unless it were beneficial, directly or indirectly, to the species acquiring it. It is not only impossible to show that the plant bug would be benefited by any such supposed poisoning of its own food, but it is at once evident that it would be seriously injured thereby, since this would amount to the prompt destruction of the very parts of the plant from which it was drawing its own food supply ".

However, the most likely explanation of the damage caused by *Lygus* bugs is the toxic reaction of a substance in the saliva of the insect when injected into the plant tissue during feeding. This theory was alluded to by Harris in 1862 (49) and Riley in 1870 (86) who spoke of the " poisonous effect " of the insect on the host plant. It has long been believed that the *Lygus* bug injects saliva into the plant while feeding (6), and confirmatory evidence has recently been secured by Flemion, Weed and Miller (39) in a very interesting experiment. These workers obtained highly radioactive *Lygus* bugs by allowing the insects to feed on sucrose solutions to which radioactive phosphorus had been added. When the insects were allowed to feed on pods of snap bean, they imparted radioactivity to the tissue at the site of feeding, thus indicating that the insect does inject oral secretions into the host tissue while feeding. By measuring the amount of radioactivity imparted, it has even been possible to estimate the quantity of oral secretion deposited (34).

Smith (93) and others have reported that there is an exudation

from the wound and swelling on the stem at the site of feeding, which would seem to indicate toxicity of a substance injected with the saliva. More positive evidence on this point was obtained when Smith found that the excised salivary glands of *Lygus pabulinus* causes a reaction in plant tissue similar to that resulting from the feeding of the insect. Therefore the available evidence supports the theory that the salivary secretions of the *Lygus* bug contain a substance toxic to plant tissue. This property is not unique to the genus *Lygus,* but is believed to occur in other members of the Miridae as well (19, 20).

It is interesting that the insects' feeding may result in destruction of the embryo in the Umbelliferae without apparent harm to the other parts of the seed. The explanation probably lies in the fact that the *Lygus* bug feeds only on succulent tender tissue. When the insect attacks the flower or very young fruit it may not have a decided preference for one certain tissue. At this stage most parts of the flower or fruit are tender and succulent, so the insect may feed on any part and cause blossom drop and reduced seed yield. In later stages of seed development, however, the embryo is still succulent, while the endosperm and seed coat have become firm (36); consequently the insect probably feeds only on the embryo.

RUDIMENTARY EMBRYOS

Another reason for poor germination in the Umbelliferae was discovered by Borthwick (11, 13). Carrot seeds were split longitudinally and examined with a binocular microscope. Many of them were found to contain a normal seed coat and endosperm, but the embryo was abnormally small in size, " sometimes so small as to be scarcely visible ". In all probability some of these were actually embryoless, but others did contain a rudimentary embryo. Flemion et al. (37, 38) have confirmed that rudimentary embryos occur in carrot and in other members of the Umbelliferae as well.

Borthwick (13) indicated that germination of carrot seed is retarded by the occurrence of rudimentary embryos. He suggested that at least some of the seeds with rudimentary embryos are viable but are dormant. A sample of carrot seed having some rudimentary embryos had a germination of 60 per cent two weeks after the beginning of the test. According to the official recommendations, carrot germination tests used to be terminated after 14 days (107),

but this sample was kept in the germinator for five months; at the end of the five-month period germination had increased to 78 per cent. Other workers have also reported delayed germination of carrot seed (1, 21, 28, 29, 59, 82, 112). Recently the official recommendation for duration of carrot germination tests has been increased to 28 days (5, 108).

There is reason to believe that delayed germination of carrot seed is a serious problem to the commercial grower. Mann and MacGillivray (73) found that non-uniform germination of carrot seed contributes to the variation in root size. This is of especial importance in California because all carrots in a field are usually dug at the same time. Carrots which are delayed in their germination encounter more competition in the field than the early-germinating carrots, so that many of the roots are too small to market.

Borthwick (13) suggested that the delayed germination in carrot seed is caused by rudimentary embryos, but he did not report conclusive evidence supporting this belief. He also reported that seed from the primary umbel gave better germination than seed from later flowering umbels, but he did not state whether there were differences in per cent of rudimentary embryos in the seed from the different umbels. Flemion and Hendrickson (32) detected no correlation between the occurrence of embryolessness and of rudimentary embryos in a given lot of seeds, but it was not absolutely proven that *Lygus* bugs are not the cause of rudimentary embryos.

Dormancy due to immature embryos can often be overcome by after-ripening (84); that is, seeds stored for a period before planting germinate better than do freshly harvested seeds. When Rose (88) classified the reasons for delayed germination of seeds in general into five categories—hard-coatedness, frosted seeds, need of after-ripening, exclusion of oxygen by the seed coat, and cause of delay not determined—he included seeds of celery, dill, parsley and parsnip in the last category. Odland (80) also obtained negative results, since one-week-old carrot seed showed 94 per cent germination, while seed 13 to 20 weeks old germinated 93 per cent. Franck and Wieringa (41) found that after-ripening did increase the rate and amount of germination of dill seed but appeared to have a detrimental effect on germination of carrot and parsley seed. Old celery seed was found to germinate better than new seed by Hopkins (60). Gardner (43) also obtained positive results with

after-ripening; one-year-old carrot seed germinated much better than fresh seed. The cause of delayed germination in the Umbelliferae is still in doubt and is worthy of further investigation.

Dormancy due to immature embryos can sometimes be overcome by exposing the seed to moderately high temperatures (23), but germination of carrot seed was not increased by soaking the seed in hot water (73). Other attempts to increase germination include scarification (43, 73), presoaking (59), increasing the oxygen supply (43), and treatment with thiourea (73) and other chemicals, but none of these improved the germination. It is interesting that exposure of carrot seeds to very high radio frequency irradiations seems to increase their germination (4, 44, 63), but there is no evidence of this being related to the problem of rudimentary embryos.

DORMANCY IN CELERY

An important reason for the poor germination sometimes encountered in celery seed lies in its dormancy when temperature and light are not suitable. The first important report on this problem was by Hicks and Key (51) in 1897. They found that celery seed planted in the dark, with the temperature kept constantly at 20° C., remained dormant but would germinate if exposed to light or to alternating temperature (30° C. six hours, 20° C. 18 hours).

There have been no further major discoveries on the problem of dormancy in celery, but their findings on the beneficial effect of light and of alternating temperature have been fully confirmed by later investigators. In 1908 Kinzel (66) reported no germination in celery seed kept in the dark for five months at 20° C., but prompt germination occurred when it was exposed to the light. This was contrary to the earlier belief that celery seed would finally germinate in the dark if kept there for several months. Hopkins (61) has stated that light has "but little influence" on germination of celery seed, but this disagrees with the findings of other workers. She found that germination of new seed was 64.1 per cent in the light and 67.3 in the dark, while that of old seed was 85.6 per cent in the light and 86.8 per cent in the dark. Possibly the reason the seeds germinated in the dark was that they were sown in a greenhouse where they received the stimulating effect of diurnal alterations in temperature, but it is still surprising that the germination

was practically identical in the dark and in the light. Niethammer-Prag (78) found that celery seed germinated in the light but not in the dark when the temperature alternation was 15–35° C. Taylor (102) found celery seed did not germinate in the dark when the temperature was constantly warm but did if the temperature was constantly cool or alternatingly cool and warm. Nutile and Canfield (79) planted celery seed in both light and darkness at constant temperatures of 20° C. and 30° C. and at alternating temperatures of 20° C. for 16 hours followed by 30° C. for eight hours, and of 10° C. for 16 hours followed by 20° C. for eight hours. Germination did occur in the dark, except when the temperature was kept constantly at 30° C., but in every case there was higher germination in the light than in the dark. Toole and Toole (105) also found that celery seeds will germinate in the dark if given alternations in temperature.

It has long been known that germination of many light-sensitive seeds is stimulated by alternations in temperature (22). Harrington (47) found that a temperature of 20° C. for 16 to 18 hours, alternating with 30° C. for six to eight hours, gave good germination, while the celery seed at constant temperature germinated well only when temperature was low (15–20° C.). Moringa (75) also obtained good germination when the temperature was alternating cool and warm or constantly cool. Hopkins (61) found celery seed was dormant when the temperature was constantly warm (30° C.) but germinated at constantly cool (15° C.) or alternating temperatures (10° and 25° C.). Taylor (102) obtained only four per cent germination at a constant temperature of 70° F., and none at 80° F. in the dark. This inhibition of germination by continuously warm temperature was overcome by a temperature period of 50° F. for two or more hours daily. Nutile and Canfield (79) obtained but 1.3 per cent germination at 30° C. in the light and none in the dark. When alternating temperatures of 20°–30° and 10°–20° C. were used, germination was 61.5 and 69.9 per cent in the light and 28.9 and 37.0 per cent in the dark, respectively. Toole and Toole (105) discovered that an alternation of 15° and 25° C. gave better results than the 20°–30° C. alternation used in official germination tests.

Germination of the members of the Umbelliferae other than celery has not been found to be inhibited by both darkness and constantly warm temperatures. The presence of light has been re-

ported to improve the germination of carrot (43, 78) and other members of the family, but, at least in the case of carrots, alternation of temperature does not increase germination (41, 47, 50, 68).

In addition to the necessity of light and correct temperature, a high moisture content is also necessary for germination of celery seed. Bailey (7) found that "sparingly watered" celery seeds germinated better than those "profusely watered", but more precise investigations by Doneen and MacGillivray (26) reveal that a high soil moisture content is a prerequisite for germination. Most seeds will germinate when the moisture content is near the permanent wilting percentage, but maximum germination of celery seeds is not realized unless the moisture content is near field capacity. Since the germination period is so critical, because of the requirements for correct moisture content and temperature, presprouting of seeds in an ideal environment has been proposed (102, 104). Taylor has suggested a method in which the seed is moistened and kept in a germinating chamber with high humidity and controlled temperature alternations of 48° F. for 16 hours and 70° F. for eight hours daily; the seed is planted in the field about eight days later when it is beginning to sprout. This procedure brought about good germination, reduction in the preemergence period (and consequently less competition from weeds) and very uniform stands at relatively low costs (102).

DORMANCY IN *Heracleum*

Extremely interesting work on the problem of dormancy in another member of the Umbelliferae, *Heracleum sphondylium* (cow-parsnip), has recently been reported by Stokes (96–99). Seeds of this plant require exposure to low temperature for germination. Seeds kept at 15° C. were dormant but those kept at 2° C. for two to three months germinated.

This requirement for after-ripening at low temperature did not appear to be affected by oxygen or carbohydrate supply, but it did appear to be related to the supply of soluble nitrogenous compounds. Chemical analyses indicated that the low temperature promotes the hydrolysis of endosperm proteins to amino acids. Seeds kept at 20° C. for eight weeks had only 0.44 mg. amino nitrogen per gm. dry weight, while those kept at 2° C. had 0.53 mg. There was also a difference in the proportions of the different amino acids. The endosperm of the seeds kept at 2° C. had an increased amount

of arginine and glycine and a reduced alanine content as compared to that of the seeds kept at 20° C. It was therefore suggested by Stokes that low temperature is necessary for germination because it brings about the formation of the particular amino acids which are required for nutrition of the embryo during germination. Additional evidence in favor of this theory was obtained by culture of excised embryos. Vigorous seedlings developed from the embryos in cultures containing glycine and arginine as the only sources of nitrogen, but development was poor when alanine and other amino acids were used in place of glycine and arginine. It was also noted in the embryo culture experiments that growth of the embryo was favored by the presence of light.

DISCUSSION

The most important seed problem in the Umbelliferae may be considered largely solved from a practical standpoint. Embryoless seeds and reduction in seed yield have been shown to be caused by the *Lygus* bug. Control of the insect during the period of flowering and seed development will improve the quality of the seed. During the last century the best means of controlling the insect was by a formidable mixture of " strong tobacco-water, quassia-water, vinegar, and cresylic soap " (86). Harris (49) in 1862 was able to recommend only such ineffective control measures as thorough irrigations so the plants would be able to " withstand the attacks of these little bugs ". Breeding varieties resistant to attack by the *Lygus* bug has been suggested (103), but this is unlikely as there is no known source of resistance in the Umbelliferae. Fortunately an efficient and economical method of control has been discovered. Application of DDT at the correct time will greatly increase the amount of seed produced and its rate of germination. In 1949 the Department of Vegetable Crops of the University of California recommended dusting of all carrot seed fields in the State with DDT. The resulting seed crop had the highest rate of germination in history (62). Handford (45) reported increasing the seed yield of carrots one and one-half times by DDT applications. The ability to control the *Lygus* bug with DDT is of especial importance now that the use of pelleted seed (16, 113) and F_1 hybrid seed of carrots (109, 110) has been proposed, since these expensive procedures would not be practicable if the germination of the seed were low.

Aside from the practical considerations, the problem of embryo-

less seeds in the Umbelliferae is also interesting from an academic standpoint. It seems astonishing that this small insect could cause a plant to produce seeds without an embryo, but the research of Flemion, Smith and others has demonstrated that one of the components of the saliva injected into the plant by the insect while feeding is apparently a toxic substance which causes disintegration of the embryo.

One unsolved problem is the cause of the embryoless seeds occasionally found by Flemion when the plants were grown in insect-free cages. The number of embryoless seeds was small in these control plants—less than one per cent—but it suggests that some factor other than the tarnished plant bug may also cause embryoless seeds. It is quite possible, of course, that eggs or undetected insects were on the plants at the time they were enclosed in cages or that the *Lygus* bug, especially nymphs, could have gotten into the cages in some way and caused the damage.

If it be true that embryoless seed is produced when *Lygus* bugs are excluded, it would be of interest to study how they occur. Embryoless seeds are known to occur occasionally by single fertilization (46, 71). Double fertilization normally occurs in the Umbelliferae (12, 64), but if triple fusion occurred without accompanying syngamy, embryoless seeds might result. This explanation seems unlikely, however, for it does not account for the cavity where the embryo normally is embedded. It seems quite evident that an embryo started to develop in these seeds, but it later degenerated. Another possibility is that of deleterious genes, as in corn, but genetic studies have not been made.

Still another unsolved problem is that of the cause of rudimentary embryos in carrots. It has been suggested (32) that the occurrence of rudimentary embryos might be the result of harvesting techniques, climatic conditions, genetical influence, toxic feeding of *Lygus* bugs or other factors. There is reason to believe that rudimentary embryos are responsible for delayed germination, so this problem is of practical interest.

It has been proven that celery seed may be dormant when kept in the dark at warm temperatures, but the dormancy can be broken by cool or alternating warm and cool temperatures or by light. Crocker (22) has written: " There is need of a very thorough and detailed chemical, microchemical and physiological study of the

effect of light upon the coats and living portions of several light-favored and light-inhibited seeds and fruits. There is also need of a similar study of the changes brought about in seeds and fruits by agents and conditions which substitute for light".

Many theories have been offered to explain the effect of light on light-sensitive seed (22), but none has been conclusively proven. One possible explanation is that of an "inhibition of inhibitors". It has been suggested that light of a certain wave-length will destroy an inhibitor of germination (30). Extracts from celery seeds have been reported to inhibit the germination of celery and other seeds (52, 101, 102), but much more evidence will be necessary to prove that the beneficial effects of light and of low and alternating temperatures on celery germination is due to inactivation of an inhibitor.

Another theory is that the beneficial effect is attributable to stimulation by light and low temperatures of the formation of metabolites required during germination. There is no conclusive evidence for celery with regard to this theory, but the research of Stokes has provided information for another member of the family, *Heracleum sphondylium*. Germination of *Heracleum*, like that of celery, is favored by low temperature and light, but *Heracleum* differs from celery in that the seeds must be treated for several months at low temperature. The results indicate that the low temperature stratification is necessary because it promotes the hydrolysis of the reserve proteins in the endosperm to the particular amino acids which are required for growth of the embryo. The explanation for the dormancy of celery seed when sown in the dark at a continuously warm temperature may be analogous to that for *Heracleum*, but there has been no report of evidence supporting or contradicting this theory.

SUMMARY

Poor germination of seeds is of common occurrence in the Umbelliferae. Probably the most important of several causes is the presence of non-viable seeds which have no embryo. Embryoless seeds have been found to result from the feeding of the *Lygus* bug on the developing seed. The insect seems to inject a toxic component of its oral secretions while feeding; this causes degeneration of the embryo. Control of the *Lygus* bug by use of insect-tight cages or

by application of insecticide greatly reduced the number of embryoless seeds and also increased the seed yield.

Rudimentary embryos have also been found in seed of the Umbelliferae, but the cause is not definitely known. It has been suggested that the seeds with rudimentary embryos are the cause of the delayed germination often encountered in carrots.

Dormancy occurs in celery seed when temperature and light are unfavorable. This dormancy can be overcome by exposing the seed to light and cool or alternating cool and warm temperatures during the germination period. Seeds of *Heracleum sphondylium* are also dormant when the temperature is warm, but several months at low temperature will break the dormancy. Low temperature seems to favor germination by promoting the breakdown of reserve proteins in the seed to the particular amino acids which are necessary for growth of the embryo.

LITERATURE CITED

1. Anonymous. Notes on germination. Assn. Off. Seed Anal., News Letter **3**(4) : 4. 1929.
2. ————. Embryoless soft chess. Assn. Off. Seed Anal., News Letter **21**(4) : 12. 1947.
3. Addicott, F. T., and V. E. Romney. Anatomical effects of *Lygus* injury to guayule. Bot. Gaz. **112:** 133–134. 1950.
4. Ark, P. A., and W. Parry. Application of high-frequency electrostatic fields in agriculture. Quart. Rev. Biol. **15:** 172–191. 1940.
5. Association of Official Seed Analysts. Rules for testing seed. Proc. Assn. Off. Seed Anal. **39:** 23–57. 1949.
6. Awati, P. R. The mechanism of suction in the potato capsid bug, *Lygus pabulinus* Linn. Proc. Zool. Soc. London **1914:** 685–733. 1914.
7. Bailey, L. H. On the influence of certain conditions upon the sprouting of seeds. New York (Cornell) Agr. Exp. Sta., Bul. 7. 1889.
8. Baker, K. F., and W. C. Snyder. Seed pitting of the lima bean by *Lygus* bugs in California. Science **103:** 500–501. 1946.
9. ————, ———— and A. H. Holland. *Lygus* bug injury of lima bean in California. Phytopath. **36:** 493–503. 1946.
10. Beneš, V. The conditions for blossoming in celery. Sbornik Ceskoslov. Akad. Zem. **21:** 54–57. 1949. [Biol. Abstr. **25:** 15035].
11. [Borthwick, H. A.]. *In:* Ann. Rep. Dir. Cal. Agr. Exp. Sta. **1928:** 68; **1929:** 59–60; **1931:** 62.
12. ————. Development of the macrogametophyte and embryo of *Daucus carota*. Bot. Gaz. **92:** 23–44. 1931.
13. ————. Carrot seed germination. Proc. Amer. Soc. Hort. Sci. **28:** 310–314. 1931.
14. Brown, E., and W. L. Goss. The germination of vegetable seeds. U. S. Dept. Agr., Bur. Plant Ind., Bul. 131. 1908.
15. ———— and ————. The germination of packeted vegetable seeds. U. S. Dept. Agr., Bur. Plant Ind., Cir. 101. 1912.
16. Carew, H. J. Pelleted seeds need more research. Farm Res. **15**(2) : 16. 1949.
17. Carlson, J. W. *Lygus* bug damage to alfalfa in relation to seed production. Jour. Agr. Res. **61:** 791–815. 1940.

18. ————. Pollination, *Lygus* infestation, genotype, and size of plants as affecting seed setting and seed production in alfalfa. Jour. Amer. Soc. Agron. **38**: 502–514. 1946.
19. CARTER, W. Injuries to plants caused by insect toxins. Bot. Rev. **5**: 273–326. 1939.
20. ————. Injuries to plants caused by insect toxins. II. Bot. Rev. **18**: 680–721. 1952.
21. COLE, GRACE M. Problems in germination testing of flower and vegetable seeds. Seed World **26**(2) : 16–17. 1929.
22. CROCKER, W. Effect of the visible spectrum upon the germination of seeds and fruits. *In:* Duggar, B. M. [ed.] Biological effects of radiation. Vol. 2: 791–827. 1936.
23. CURTIS, O. F., and D. G. CLARK. An introduction to plant physiology. 752 pp. 1950.
24. DAVIS, G. C. Celery insects. Mich. Agr. Exp. Sta., Bul 102. 1893.
25. DEMEREC, M. Heritable characters of maize. XV. Germless seed. Jour. Hered. **14**: 297–300. 1923.
26. DONEEN, L. D., and J. H. MACGILLIVRAY. Germination (emergence) of vegetable seeds as affected by different soil moisture conditions. Plant Physiol. **18**: 524–529. 1943.
27. DOXTATOR, C. W. The effect of *Lygus* control on the production of elite seed. Proc. Amer. Soc. Sugar Beet Technol. **5**: 499–501. 1948.
28. DURFEE, BERTHA. Carrot seed germination observations. Assn. Off. Seed Anal., News Letter **22**(3) : 17–18. 1948.
29. ELLIOTT, G. A. Germination of carrot seed. Assn. Off. Seed Anal., News Letter **3**(12) : 12–15. 1929.
30. EVENARI, M. Germination inhibitors. Bot. Rev. **15**: 153–194. 1949.
31. FLEMION, FLORENCE. *Lygus* bugs in relation to the occurrence of embryoless seeds in the Umbelliferae. Science **109**: 364–365. 1949.
32. ———— and ESTHER T. HENRICKSON. Further studies on the occurrence of embryoless seeds and immature embryos in the Umbelliferae. Contrib. Boyce Thompson Inst. **15**: 291–297. 1949.
33. ———— and BETTY T. MACNEAR. Reduction of vegetative growth and seed yield in umbelliferous plants by *Lygus oblineatus*. Contrib. Boyce Thompson Inst. **16**: 279–284. 1951.
34. ————, L. P. MILLER and R. M. WEED. An estimate of the quantity of oral secretion deposited by *Lygus* when feeding on bean tissue. Contrib. Boyce Thompson Inst. **16**: 429–433. 1952.
35. ———— and JUNE OLSON. *Lygus* bugs in relation to seed production and occurrence of embryoless seeds in various umbelliferous species. Contrib. Boyce Thompson Inst. **16**: 39–46. 1950.
36. ————, HARRIET POOLE and JUNE OLSON. Relation of *Lygus* bugs to embryoless seeds in dill. Contrib. Boyce Thompson Inst. **15**: 299–310. 1949.
37. ———— and GLORIA UHLMANN. Further studies of embryoless seeds in the Umbelliferae. Contrib. Boyce Thompson Inst. **14**: 283–293. 1946.
38. ———— and ELIZABETH WATERBURY. Embryoless dill seeds. Contrib. Boyce Thompson Inst. **12**: 157–161. 1941.
39. ————, R. WEED and L. P. MILLER. Deposition of P^{32} into host tissue through the oral secretions of *Lygus oblineatus*. Contrib. Boyce Thompson Inst. **16**: 285–294. 1951.
40. FORBES, S. A. The tarnished plant bug (*Lygus lineolaris* Beauv.). Illinois State Entomologist, 13th Rep. on Noxious and Beneficial Insects, pp. 115–135. 1884.
41. FRANCK, W. J., and G. WIERINGA. Artificial drying and low temperature as means employed in obtaining an increase in germination of some vegetable seeds. Proc. Assn. Off. Seed Anal. **19**: 24–27. 1928.

42. FRASER, S., J. W. GILMORE and C. F. CLARK. Culture and varieties of roots for stock feeding. New York (Cornell) Agr. Exp. Sta., Bul. 244. 1907.
43. GARDNER, W. A. Effect of light on germination of light-sensitive seeds. Bot. Gaz. **71**: 249–288. 1921.
44. GOUBAREFF, A. N. The high frequency oscillator: Its design and use in the study of stimulating and lethal effects on certain biological materials. Thesis, Univ. Cal., Berkeley. 1938.
45. HANDFORD, R. H. *Lygus campestris* (L.): A new pest of carrot seed plants. Canad. Entom. **81**: 123–126. 1949.
46. HARLAN, H. V., and M. N. POPE. Some cases of apparent single fertilization in barley. Amer. Jour. Bot. **12**: 50–53. 1925.
47. HARRINGTON, G. T. The use of alternating temperatures in the germination of seeds. Jour. Agr. Res. **23**: 295–332. 1923.
48. HARRINGTON, J. F. Effect of spacing and size of root on carrot seed yield and germination. Proc. Amer. Soc. Hort. Sci. **58**: 165–167. 1951.
49. HARRIS, T. W. A treatise on some of the insects injurious to vegetation. 640 pp. 1862.
50. HARTLEB, R., and A. STUTZER. Untersuchunger über die Methode der Samenprüfung, insebesondere diejenige der Grassämereien. Jour. Landw. **45**: 43–60. 1897.
51. HICKS, G., and S. KEY. Additional notes on seed testing. U. S. Dept. Agr., Yearbook **1897**: 441–452. 1898.
52. HICKS, SELMA S., D. M. DOTY and F. W. QUACKENBUSH. A germination inhibitor from apple and celery seeds Fed. Proc. **10**: 196–197. 1951.
53. HILL, L. C. Further studies of tarnished plant bug injury to celery. Jour. Econ. Entom. **26**: 148–150. 1933.
54. HILLS, O. A. Isolation-cage studies of certain hemipterous and homopterous insects on sugar beets grown for seed. Jour. Econ. Entom. **34**: 756–760. 1941.
55. ————. Comparative ability of several species of *Lygus* and the Say stinkbug to damage sugar beets grown for seed. Jour. Agr. Res. **67**: 389–394. 1943.
56. ———— and V. E. ROMNEY. Progress report on investigations of insects affecting sugar beets grown for seed in Arizona and New Mexico. Proc. Amer. Soc. Sugar Beet Technol. **3**: 468–470. 1942.
57. ———— and E. A. TAYLOR. *Lygus* damage to beet seed in varying stages of development. Proc. Amer. Soc. Sugar Beet Technol. **5**: 502–503. 1948.
58. ———— and ————. *Lygus* damage to sugar beet seed in various stages of development. Proc. Amer. Soc. Sugar Beet Technol. **6**: 481–487. 1950.
59. HOEFLE, OLIVE M. Results of a study of *Daucus carota* seeds. Proc. Assn. Off. Seed Anal. **21**: 35–36. 1929.
60. HOPKINS, ELIZABETH F. Studies on the germination of celery seed. Proc. Assn. Off. Seed Anal. **18**: 47–49. 1926.
61. ————. Further studies of celery seed germination. Proc. Assn. Off. Seed Anal. **19/20**: 69–70. 1928.
62. HUTCHISON, C. B., ed. Research program, College of Agriculture, Univ. of Calif., 1949/1950 (p. 129). 399 pp. 1950.
63. JONAS, H. Some effects of very high radio frequency irradiations on the germination and metabolism of certain small seeds. Thesis, Univ. Cal., Berkeley. 1950.
64. JURICA, H. S. A morphological study of the Umbelliferae. Bot. Gaz. **74**: 292–306. 1922.

65. KING, W. V., and W. S. COOK. Feeding punctures of Mirids and other plant-sucking insects and their effect on cotton. U. S. Dept. Agr., Tech. Bul. 296. 1932.
66. KINZEL, W. Lichtkeimung. Einige bestätigende und ergänzende Bemerkungen zu den vorläufigen Mitteilungen von 1907 und 1908. Ber. Deut. Bot. Ges. **26a**: 631–645. 1908.
67. KONDŌ, M., and S. ISSHIKI. The presence of abnormal rice kernels which are either germless or which possess two embryos. Ber. Ōhara Inst. Landw. Forsch. **6**: 515–524. 1934. [Exp. Sta. Rec. **74**: 319].
68. KOTOWSKI, F. Temperature alternation and germination of vegetable seed. Acta Soc. Bot. Polon. **5**(1) : 71–78. 1927.
69. LYON, MILDRED E. Embryoless seeds in cereals. Science **67**: 652. 1928.
70. ————. The occurrence and behavior of embryoless wheat seed. Jour. Agr. Res. **36**: 631–637. 1928.
71. MAHESWARI, P. An introduction to the embryology of Angiosperms. 453 pp. 1950.
72. MANGELSDORF, P. C. The genetics and morphology of some endosperm characters in maize. New York (Cornell) Agr. Exp. Sta., Bul. 279. 1926.
73. MANN, L. K., and J. H. MACGILLIVRAY. Some factors affecting the size of carrot roots. Proc. Amer. Soc. Hort. Sci. **54**: 311–318. 1949.
74. MCGREGOR, E. A. *Lygus elisus:* A pest of the cotton regions in Arizona and California. U. S. Dept. Agr., Tech. Bul. 4. 1927.
75. MORINGA, T. Effect of alternating temperatures upon the germination of seeds. Amer. Jour. Bot. **13**: 141–158. 1926.
76. MORRILL, A. W. Insect pests of interest to Arizona cotton growers. Ariz. Agr. Exp. Sta., Bul. 87 : 172–205. 1918.
77. MUNN, M. T., and C. E. HEIT. Embryoless seeds of the Umbelliferae. Assn. Off. Seed Anal., News Letter **15**(4) : 10. 1941.
78. NIETHAMMER-PRAG, A. VON. Licht, Dunkelheit und Strahlung als Faktoren bei der Samen-Keimung. Tab. Biol. Per. **10**: 45–77. 1934.
79. NUTILE, G. E., and A. P. CANFIELD. Effect of temperature and light on the germination of celery seed. Assn. Off. Seed Anal., News Letter **24**(2) : 20–22. 1950.
80. ODLAND, M. L. Observations on dormancy in vegetable seeds. Proc. Amer. Soc. Hort. Sci. **35**: 562–565. 1937.
81. OSWALD, W. L. Seed laboratory report for 1910 and 1911. Minn. Agr. Exp. Sta., Bul. 127. 1912.
82. PATTERSON, MARY N. Germination studies of carrot seed. Proc. Assn. Off. Seed Anal. **23**: 73–75. 1931.
83. PIETERS, A. J. Testing seeds at home. U. S. Dept. Agr., Yearbook **1895**: 175–184. 1896.
84. PORTER, R. H. Recent developments in seed technology. Bot. Rev. **15**: 221–344. 1949.
85. RICHARDSON, J. K. Studies on blackheart, soft rot, and tarnished plant bug injury of celery. Canad. Jour. Res., C, **16**: 182–193. 1938.
86. RILEY, C. V. The tarnished plant bug, *Capsus oblineatus* Say. 2nd Ann. Rept. on Noxious, Beneficial, and Other Insects of the State of Missouri, pp. 113–115. 1870.
87. ROMNEY, V. E., G. T. YORK and T. B. CASSIDY. Effect of *Lygus* spp. on seed production and growth of guayule in California. Jour. Econ. Entom. **38**: 45–50. 1945.
88. ROSE, D. H. A study of delayed germination in economic seeds. Bot. Gaz. **59**: 425–444. 1915.
89. SANDERS, MARY E. Embryo development in four *Datura* species following self and hybrid pollinations. Amer. Jour. Bot. **35**: 525–532. 1948.

90. SASS, J. E., and G. F. SPRAGUE. The embryology of "germless" maize. Iowa State Coll., Jour. Sci. **24**: 209–218. 1950.
91. SAUNDERS, W. Testing the viability of seeds. Canada Exp. Farms, Rpt. **1892**: 41–42. 1892.
92. SHULL, W. E. An investigation of the *Lygus* species which are pests of beans (Hemiptera, Miridae). Idaho Agr. Exp. Sta., Res. Bul. 11. 1933.
93. SMITH, K. M. Investigation of the nature and cause of the damage to plant tissue resulting from the feeding of Capsid bugs. Ann. Appl. Biol. **7**: 40–55. 1920.
94. SORENSON, C. J. *Lygus hesperus* Knight and *Lygus elisus* van Duzee in relation to alfalfa seed production. Utah Agr. Exp. Sta., Bul. 284. 1939.
95. STITT, L. L. Three species of the genus *Lygus* and their relation to alfalfa seed production in southern Arizona and California. U. S. Dept. Agr., Tech. Bul. 741. 1940.
96. STOKES, PEARL. A physiological study of embryo development in *Heracleum sphondylium* L. I. The effect of temperature on embryo development. Ann. Bot. (n.s.) **16**: 439–447. 1952.
97. ————. A physiological study of embryo development in *Heracleum sphondylium* L. II. The effect of temperature on after-ripening. Ann. Bot. (n.s.) **16**: 571–576. 1952.
98. ————. A physiological study of embryo development in *Heracleum sphondylium* L. III. The effect of temperature on metabolism. Ann. Bot. (n.s.) **17**: 157–173. 1953.
99. ————. The stimulation of growth by low temperature in embryos of *Heracleum sphondylium* L. Jour. Exp. Bot. **4**: 222–234. 1953.
100. STONE, G. E. Seed separation and germination. Mass. Agr. Exp. Sta., Bul. 121. 1908.
101. STOUT, M., and B. TOLMAN. Factors affecting the germination of sugar-beet and other seeds with special reference to the toxic effects of ammonia. Jour. Agr. Res. **63**: 687–713. 1941.
102. TAYLOR, C. A. Some factors affecting germination of celery seed. Plant Physiol. **24**: 93–102. 1949.
103. TAYLOR, T. H. C. *Lygus simonyi* Reut. as a cotton pest in Uganda. Bul. Entom. Res. **36**: 121–148. 1946.
104. THOMPSON, H. C. Vegetable crops. 4th ed. 611 pp. 1949.
105. TOOLE, E. H., and VIVIAN K. TOOLE. Methods of testing celery seed in relation to seed storage problems. Proc. Assn. Off. Seed Anal. **41**: 62–65. 1951.
106. TROOP, J. Some injurious insects of the year. Trans. Ind. Hort. Soc. **1891**: 73. 1892.
107. U. S. Department of Agriculture. Rules and recommendations for testing seeds. U. S. Dept. Agr., Cir. 480. 1938.
108. ————. Manual for testing agricutural and vegetable seeds. U. S. Dept. Agr., Agr. Handb. **30**. 1952.
109. WELCH, J. E., and E. L. GRIMBALL, JR. Male sterility in the carrot. Science **106**: 594. 1947.
110. ———— and ————. Investigation on variation of carrot root sizes: Possibilities for the development of a hybrid carrot with root size uniformity under study. Calif. Agr. **3**(10): 8, 12. 1949.
111. WENTZ, J. B. The inheritance of germless seeds in maize. Iowa Agr. Exp. Sta., Res. Bul. 121. 1930.
112. WILKES, MAXINE. Germination of carrot seed. News Letter, Assn. Off. Seed Anal. **3**(5): 3–4. 1929.
113. WORK, P. Preliminary facts on coated seed. Mkt. Grow. Jour. **79**(5): 16–19. 1950.

COMPRESSION WOOD IN CONIFERS AS A MORPHOGENETIC PHENOMENON

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INTRODUCTION

Compression wood—otherwise known as " redwood ", " reaction wood ", " Rotholz ", " Druckholz " and " bois rouge "—is of common occurrence in conifers. Much attention has been given to its occurrence, formation, and properties, yet the mechanism by which it is laid down is poorly understood. The present paper represents an effort to summarize briefly and succinctly our present knowledge of the formation and function of compression wood in conifers.

A fairly complete bibliography is appended. Several references have been omitted, for they deal only casually with the phenomenon, as well as others dealing with compression wood only as a defect in wood utilization. Apart from these omissions the bibliography is much nearer complete than any other in the literature. No effort, however, will be made to present a complete review of the literature, although practically all of the references cited have been examined in the preparation of this paper. Several of the principal references have been reviewed in English (Büsgen and Münch, 1929; Kienholz, 1930; Sinnott, 1952). It is felt that more is to be gained by extracting and emphasizing what appear to be the major points.

Lengthy though the bibliography is, it covers only a small part of the relevant literature, the part dealing expressly with compression wood. As with any other morphogenetic phenomenon, compression wood can not be considered as an isolated subject, but must be treated in relation to the rest of the plant organization. Compression wood is a tropic phenomenon, and the whole literature on geotropism and probably photoperiodism as well is relevant. Similarly attention should be paid to the literature on mechanical factors, such as induced torsion and compression; on eccentric growth; on tension wood, the related phenomenon in angiosperms; and on gravity effects other than geotropism. There

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is evidence that growth substances may play a part in causing the formation of compression wood, and a study of the related literature in this field is called for. Finally compression wood results from a change in the process of cell wall formation, and the vast literature dealing with this process should also be consulted.

OCCURRENCE

The occurrence of compression wood was first treated in detail by Mer (1887*a*, 1887*b*), Hartig (1896, 1899, 1901) and Cieslar (1896). It is known to occur:

1. Normally on the underside of lateral branches in conifers.
2. On the underside of the main stem in leaning trees.
3. On the underside of the main stem of living fallen trees, even though the stem is supported by the ground throughout its length.
4. On the reverse side of the stem or branch after initial abnormal curvature has been overcorrected, apparently by compression wood on the original under side.
5. Rarely as spiral bands in apparently erect trees, the bands continuing to develop throughout the life of the tree and causing as many as seven whirls of compression wood in the cross-section (Fabricius, 1932; Hartmann, 1932; Douglass, 1940; Fritz, 1940; correspondence, U. S. Forest Products Lab.). Cases have been reported from Sweden, Alaska and Quebec, all in spruce (*Picea* spp.). Compression wood always occurred at point of maximum diameter growth.
6. On the lower side of naturally occurring crooks and deformations in the stems of trees (Hartig, 1896; Spurr and Friend, 1941 and others).
7. In the normal stem which is apparently straight, but below natural or artificially induced deformations and obviously related to them (Cieslar, 1896; Hartmann, 1932).
8. More in fast-growing than slow-growing trees. For example, Pillow and Luxford (1937) found that with ponderosa pine (*Pinus ponderosa*) in the Black Hills, trees with moderate lean (3–5 degrees) which had recently formed compression wood had a rate of diameter growth more than twice as great as that in trees of similar lean in which compression wood formation was not noticeable. Similarly trees with pronounced lean (more than 5½ degrees) not forming recognizable compression wood were non-vigorous and

increased in diameter at a rate of less than one-fifth that of the trees which were forming recognizable compression wood.

9. In trees exposed to a strong prevailing wind, on the opposite or lee side (Hartig, 1899). Haller (1935) showed that this occurred even when the trees were standing vertically and also that diameter growth was at a maximum on the side where compression wood occurred.

10. In the upper boles of thinned stands (Hartig, 1896). Paul and Meagher (1949) found that when 200-year-old trees of *Pinus ponderosa* were released from competition by partial cutting, the resulting accelerated diameter growth was accompanied by a somewhat greater formation of compression wood.

11. On stems whose crowns are protected from prevailing winds, but which face a clearing, on that side facing the clearing (Haller, 1935).

12. On the outer sides of stems standing very close to one another. Such stems may be vertical but frequently have a small amount of lean and exhibit eccentric growth (Haller, 1935). Originally shown by Hartig, 1899.

13. Under ridges of eastern white pine (*Pinus strobus*) trunks on the leeward side of trees which survived the 1938 hurricane in New Hampshire (Mergen and Winer, 1952). These ridges were found to correspond with compression wood failures covered by broad layers of compression wood.

The above points deal primarily with naturally-occurring compression wood. In addition, compression wood has been induced by a large number of workers confirming most of the above observations and adding the following points:

14. All around a tree when revolved one-quarter turn every 12 hours (Burns, 1920). Apparently also by White (1908).

15. On the physically lower side in artificially deformed stems (Ewart and Mason-Jones, 1906; White, 1908; Burns, 1920; and many others).

16. Toward the focus of gravitational attraction when the gravitational field relative to the axis of the tree is reversed. In other words, if a tree is grown upside-down, compression wood will form on the morphologically upper side of the branches which are physically the lower sides (Jaccard, 1920; Wershing and Bailey,

1942). Similarly, if grown on a revolving table, compression wood will form on the outer side of the stem (Jaccard, 1939).

17. On the upper side of upward-curving branches after the portion of the tree above them has been removed (Petersen, 1914).

18. Apparently in association with stem swellings produced by auxin application (Wershing and Bailey, 1942). Onaka (1949) experimented with indole-3-acetic acid and naphthalene acetic acid treatments in *Pinus, Picea* and other conifers. A typical compression wood structure developed, and the axis of the tree bent away from the treated side when the reagent was applied to one side only. Fraser (1952) also applied heteroauxin to pine (*Pinus strobus*) and found that a "proper" concentration stimulated cambial activity and continuous production of spring wood, but that a greater concentration produced "redwood" or compression wood.

19. On the upper side (both gravitationally and morphologically) of branches which have been forced upward from their natural position (Hartmann, 1932).

20. Laterally on branches which have been forced laterally from their natural position (Sinnott, 1952).

It should finally be pointed out that compression wood does not occur in the main stem when the plant is exactly inverted (Hartmann, 1932), when a tree is rotated rapidly on a clinostat (White, 1908, found that the minimum period for response to gravity was two hours), in an artificial wind (Burns, 1920), or when two-thirds of the circumference of the crown is artificially trimmed off (Burns, 1920).

The above discussion records only the principal reports. Many of the observations were made or confirmed by others than those cited, but an effort has been made to give the main references.

PROPERTIES AND FUNCTION

The properties of compression wood have been studied in detail and are summarized by Pillow and Luxford (1937), Wershing and Bailey (1942), Onaka (1949), and series of papers by Jaccard, Münch and Trendelenburg. It may be pointed out that, in addition to its other well-known properties, compression wood changes its longitudinal length greatly with changes in moisture content, even to the extent that coniferous branches curve sharply upward

when the relative humidity is high and droop sharply when the humidity is low (Anon., 1924).

There seems to be little doubt but that the function of compression wood in the tree is to exert compression so as to counteract forces tending to deform the tree. Gravitation is commonly such a force which always affects branches and also affects the main stem when it is deformed or moved from a vertical position.

That compression wood forms in response to a deforming force in advance of noticeable deformation is indicated by the presence of compression wood in many straight and vertical stems (points 5, 9, 10, 11 and 16 above).

The appropriateness of the structure of compression wood to assist in counteracting forces, and especially to erect bent and leaning stems, is pointed out in various papers by Jaccard, Münch and Trendelenburg.

That compression wood may affect the axis of even large stems has been demonstrated (Engler, 1918; Millett, 1944; and unpublished data of Lutz). Engler cites 67-year-old spruce (*Picea abies*) bent 20 degrees by a landslide and afterwood exhibiting correctional bending at a point where the stem was nine inches in diameter. The amount of correction is related to the growth in height and diameter, as demonstrated by unpublished work of Spurr.

GOVERNING FACTORS

Any number of controlling factors—gravity, wind, requirements of water circulation, longitudinal compression, lateral compression, nutrition, growth substances, galvano-tropism, growth rate—have been suggested as causes of compression wood. The importance of most of these have been minimized by published research. Clarke (1939) gives a clear statement of present views:

"The consensus of present opinion is that reaction wood is stimulated mainly by the force of gravity, which is apparently able to exert influence through the medium of weight, and through such channels as negative geotropism. Although suggestions have been made of a polar effect on the distribution of food-supplies and of growth substances, the mode of action remains obscure".

From the above discussion, however, it should be apparent that while gravity is the deforming force most frequently associated with compression wood, it is by no means the only force. Indeed,

gravity has no effect on the tissue development in this case except when it exerts a deforming as opposed to a normal force. We may conclude, therefore, that compression wood is a response to a deforming force, and that this deforming force is most frequently gravity, but may be of another character.

As to the mechanics of transmittal of the force to the tissue, anyone familiar with the behaviour of growth substances in plants can not fail to see a close similarity between the known habits of concentration of auxin and the occurrence of compression wood. The geotropic relations, the disturbance of normal behaviour by decapitation of the leader or by disturbance of the normal morphological position of parts of the plants, the occurrence of compression wood below the point of curvature in the straight part of the stem,—these and other factors indicate a close correlation between growth substances and compression wood.

Unfortunately little has been done experimentally with this problem. Wershing and Bailey (1942) were apparently able to induce compression wood by auxin application to *Pinus strobus* seedlings, but were not able to demonstrate that the auxin application was the causal factor. Indeed it is much more likely that the compression wood was formed in response to the deformation caused by the swelling induced in the stem by the auxin application. In other words, auxin in this case was very likely the deforming force, not the direct regulator.

Five investigators (Czaja, 1931; Zimmerman, 1936; Mirov, 1941; Onaka, 1949; Fraser, 1952) have dealt with auxin concentration in coniferous stems. Mirov, who summarized the work of his two predecessors, found evidence that auxin moved downward in *Pinus ponderosa* and *Pinus torreyana*. In developing shoots he found the lowest auxin concentration in the top five mm and the maximum at the base of the present year's shoot, and thus concluded that under the conditions of his experiments, the highest concentration of growth hormone in a given plant does not coincide with the region of most vigorous growth. As between trees, however, he found that hormone concentration was always higher in fast-growing than in slow-growing young pines. Since environmental conditions were closely controlled, this would indicate that hormonal concentration is an hereditary character. More applicable to the present study, it would further suggest that auxin con-

centration is associated with compression wood, since the region of compression wood formation always coincides with the region of maximum diameter growth in eccentric stems. Onaka (1949) found that the greater amounts of auxin in leaning coniferous stems were on the lower side. He concluded that " the direct cause of compression wood formation is the accumulation of auxin, and the physiological meaning of such wood lies in acting the growth movement of tree growth ".

It is not difficult to imagine the role of auxin in causing compression wood. Normally auxin concentrations in stem tissues cause tissue elongation. If such elongation is effectively prevented by compression caused by a leaning tree or similar structural effect, the metabolic balance of the tissue might well be thrown out of balance and the result could easily be a different type of structure instead of merely a bigger structure. Water content of the compression wood structure might well be the mechanism by which the deformation of stems is actually brought about by compression wood.

SUMMARY

Although much has been done with compression wood, its basic causes have only recently been investigated. It seems quite clear that compression wood is formed indirectly as a counteractant to forces tending to deform a tree in any way. It seems equally clear that compression wood is actually under great compression and actually tends to straighten the tree or otherwise overcome the deformation, be the deformation actual or incipient. Finally it seems quite probable that auxin is the regulator which sets off the intracellular reaction that causes formation of the anomaly.

BIBLIOGRAPHY

Anon. 1924. Spruce limb serves as a humidity indicator. West Coast Lumberman **44**(536): 26b. 1 fig.

Burns, G. P. 1920. Eccentric growth and the formation of redwood in the main stem of conifers. Vt. Agr. Exp. Sta., Bull. 219: 1–16.

Büsgen, M., and E. Münch. 1929. The structure and life of forest trees. [Eng. trans. by Thomas Thomson]. 436 pp.

Cieslar, A. 1896. Das Rotholz der Fichte. Centralblatt für der gesammte Forstwesen (Austria) **22**: 149–165.

Clarke, S. H. 1939. Stresses and strains in growing timber. Forestry **13**: 68–79.

Czaja, A. T. 1931. Der Nachweis des Wachstoffes bei Holzflanzen. Ber. Deut. Bot. Ges. **52**: 267–271.

DADSWELL, H. E., and L. F. HAWLEY. 1929. Chemical composition of wood in relation to physical characteristics. Ind. Eng. & Chem. **21**: 973. [Not seen].

———— and I. LANGLANDS. 1933. Compression wood in hoop and bunya pine. Jour. Council Sci. & Ind. Res., May, 1933: 120–124.

———— and A. B. WARDROP. 1949. What is reaction wood? Aust. For. **13**: 22–23.

DOUGLASS, A. E. 1939–40. Examples of spiral compression wood (in spruce from Sweden and Alaska). Tree Ring Bull. 6: 21–22.

ENGLER, A. 1918. Tropismen und exzentrisches Dickenwachstum der Bäume. Ein Beitrag zur Physiologie und Morphologie der Holzgewächse. 106 pp. 30 fig. Schr. Stift. Schnyder von Wartensee. Zurich. [Not seen. Reviewed by Büsgen in Zeits. Forst- u. Jagdwesen **51**: 43–44. 1919; and by Bailey in Bot. Gaz. **70**: 159–162].

EWART, A. J., and A. G. MASON-JONES. 1906. The formation of red wood in conifers. Ann. Bot. **20**: 201–204.

FABRICIUS. 1932. Ein merkwürdiger Fall von Rotholzbildung. Forstwiss. Centralblatt **76**: 422–424.

FRASER, D. E. 1952. Initiation of cambial activity in some forest trees in Ontario. Ecology **33**: 259–273.

FRITZ, E. 1940. Problems in dating rings of California coast redwood. Tree Ring Bul. 6: 19–20.

GROSSENBACHER, J. G. 1916. Periodicity and distribution of radial growth in trees and their relation to the development of annual rings. Trans. Wis. Acad. Sci. Arts & Letters **18**: 1–77.

HÄGGLUND, E., and S. LJUNGGREN. 1933. Untersuchungen des Rotholzes von Fichte. I. Die Chemische Zusammensetzung des Rotholzes. Särtryck Svensk. Kemisk. Tidskr. **45**: 123–129. [Not seen].

HALLER, B. 1935. Uurimusi okaspuude ekstsentrilisest jamedusekasvust. (Untersuchungen über das exzentrische Dickenwachstum der Nadelholzstamme.) [German summary]. Tartu Ülikooli Metsaosakonna toimetused. No. 24. pp. viii + 223. [Not seen.]

HARTIG, R. 1896. Das Rotholz der Fichte. Forstlich-naturwiss. Zeits. **5**: 96–109, 157–169.

————. 1899. Ueber die Ursachen excentrischen Wuchses der Waldbäume. Centbl. Gesam. Forstw. **25**(7): 291–307.

————. 1901. Holzuntersuchungen Altes und Neues.

HARTMANN, F. 1932. Untersuchungen über Ursachen und Gesetzmässigkeit exzentrischen Dickenwachstums bei Nadel- und Laubbäumen. Forstw. Central. **54**(15) 497–517, (16) 547–566, (17) 581–590, (18) 622–634. 21 fig. Biol. Abst. **7**(5): 1044.

————. 1932. Zu "Ein merkwürdiger Fall von Rotholzbildung". Forstw. Central. **54**: 494–496.

————. 1942. Das statische Wuchsgesetz bei Nadel- und Laubbäumen. 111 pp.

————. 1943. Die Frage der Gleichgewichtsreaktion von Stamm und Wurzel heimicher Waldbäume. Biologia Generalis **17**: 367–418.

HOLMES, W. H. 1944. The amount and distribution of compression wood in leaning white pine trees. Yale School For., unpub. master's thesis. 28 pp.

JACCARD, P. 1912. Über Abnorme Rotholzbildung. Ber. Deut. Bot. Ges. **30**: 670–678.

————. 1919. Nouvelles recherches sur l'accroisement en épaisseur des arbres: Essai d'une théorie physiologique de leur croissance concentrique et excentrique. Pub. Foundation Schnyder von Wartensee Zürich. 23: xii + 200 pp. 32 plates, 75 fig. [Not seen. Reviewed by Bailey in Bot. Gaz. **70**: 159–162].

————. 1920. Inversion de l'excentricité des branches produite experimentalement. Rev. Gén. Bot. **32:** 273–281.
————. 1922. Mécanisme du rédressement géotropique de la tige des arbes. Rev. Gén. Bot. **34:** 385–398.
———— and A. Frey. 1928. Einfluss von mechanischen Beanspruchungen auf die Micellarstructur, Verholzung und Lebensdauer der Zug- und Druckholzelemente beim Dickenwachstum der Bäume. Jahr. Wiss. Bot. **68:** 844–866.
———— and ————. 1928. Quellung, Permeabilität und Filtrationswiderstand des Zug- und Druckholzes van Laub- und Nadelbäumen. Jahr. Wiss. Bot. **69:** 549–571.
————. 1938. Exzentrisches Dickenwachstum und anatomisch-histologische Differenzierung des Holzes. Ber. Schweiz. Bot. Ges. **48:** 491–537. [Not seen].
————. 1939. Tropisme et bois de reaction provoqué par la force centrifuge. Bull. Soc. Bot. Suisse **49:** 135–147.
Jacobs, M. R. 1945. The growth stresses of woody stems. Austral. Common., For. Bur., Bull. 28. 67 pp.
Johnson, B., and R. W. Hovey. 1918. The determination of cellulose in wood. Jour. Soc. Chem. Ind. **37:** 132T–137T. [Not. seen].
Kienholz, R. 1930. The wood structure of a pistol-butted mountain hemlock. Am. Jour. Bot. **17:** 739–764.
Konontschuk, P. 1888. Die örtliche und einseitige Hartringigkeit der Kiefer und Fichte. Jahrb. Petersb. Forstinst. **2:** 41–56. [Not seen. Abstracted in Zeits. Forst. Jagdwes. **13:** 172. 1891].
Mer, E. 1887. De la formation du bois rouge dans le Sapin et l'Épicéa. Compt. Rend., Acad Sci. [Paris] **104:** 376–378.
————. 1887. De a formation du bois rouge. Forêt **3:** 113–114. [Not seen].
Millett, M. R. O. 1944. Lean and ellipticity of stems of Monterey pine in the Australia Capital Territory. Leafl. Commonw. For. Bur. Aust. 60. 10 pp.
Mirov, N. T. 1941. Distribution of growth hormones in shoots of two species of pine. Jour. For. **39:** 457–464.
Mergen, F., and H. I. Winer. 1952. Compression failures in the boles of living conifers. Jour. For. **50:** 677–679.
Mork, Elias. 1928. Om Tennar [On compression wood]. [Not seen. Reviewed in Jour. For. **29:** 599–601].
Münch, E. 1937. Entstehungsursachen und Wirkung des Druck- und Zugholzes der Baüme. Forstl. Wochensch. Silva **25**(44) : 337–341, (45) : 345–350. [Not seen. Reviewed by R. Trendelenburg in Holz als Roh- und Werkstoff **1:** 358–359. 1938].
————. 1938. Statik und Dynamik des schraubigen Baues der Zellwand, besonders des Druck- und Zugholzes. Flora **132:** 357–424.
————. 1938. Untersuchungen über die Harmonie in der Baumgestalt. Jahr. Wiss. Bot. **86:** 581–673.
————. 1939. Weitere Untersuchungen über Druckholz und Zugholz. Flora **134:** 45–57.
Onaka, F. 1949. (Studies on compression and tension wood). Wood Research. Kyoto. No. 1, 88 pp. [Japanese, English sum.].
Paul, B. H., and G. Meagher. 1949. Growth-quality study of ponderosa pine. West Coast Lumberman **76**(6) : 82, 84, 93–94.
Petersen, O. G. 1914. Forandring i. Vedbygning ved Grenrejaning has Rødgran (*Picea excelsa*). Bot. Tidsskr. (Denmark) **33:** 354–361.
Phillips, E. W. J. 1937. The occurrence of compression wood in African pencil cedar. Empire For. Jour. **16**(1) : 54–57.
Pillow, M. Y. 1930. Compression wood as a cause of distortion of softwood lumber. Jour. For. **28:** 1173–1177.

————. 1931. Compression wood records hurricane. Jour. For. **29**: 575–578.
———— and R. F. LUXFORD. 1937. Structure, occurrence and properties of compression wood. U. S. Dept. Agr., Tech. Bull. 546. 32 pp.
————. 1941. A new method of detecting compression wood. Jour. For. **39**: 385–387.
ROTHE, G. 1930. Druckfestigkeit und Druckelastizität des Rot- und Weissholzes der Fichte. Tharandter Forstliches Jahrbuch **81**: 204–231.
SINNOTT, E. W. 1952. Reaction wood and the regulation of tree form. Am. Jour. Bot. **37**: 69–78.
SONNTAG, P. 1904. Ueber die mechanischen Eigenschaften des Roth- und Weissholzes der Fichte und anderer Nadelhölzer. Jahrb. Wiss. Bot. **39**: 71–105.
SPURR, S. H., and R. B. FRIEND. 1941. Compression wood in weeviled northern white pine. Jour. For. **39**: 1005–1006.
TRENDELENBURG, R. 1932. Über die Eigenschaften des Rot- oder Druckholzes der Nadelhölzer. Allg. Forst. u. Jagd. Ztg. **108**: 1–14.
————. 1939. Das Holz als Rohstoff. Seine Entstehung, stoffliche Beschaffenheit und chemische Verwertung. 435 pp. [Not seen].
URSPRUNG, A. 1906. Die Erklarungsversuche des excentrischen Dickenwachstums. Biol. Cent. **26**: 257–272.
WARDROP, A. B., and H. E. DADSWELL. 1950. The nature of reaction wood. II. The cell wall organization of compression wood tracheids. Aust. Jour. Sci. Res. **3B**: 1–13.
———— and ————. 1952. The nature of reaction wood. III. Cell division and cell wall formation in conifer stems. Aust. Jour. Sci. Res. **5B**: 385–398.
WERSHING, H. F., and I. W. BAILEY. 1942. Seedlings as experimental material for the study of "redwood" in conifers. Jour. For. **40**: 411–414.
WHITE, JEAN. 1908. The formation of redwood in conifers. Proc. Royal Soc. Victoria, N.S. **20**: 107–124.
ZIMMERMAN, W. A. 1936. Untersuchungen über die raumliche und zeitliche Verteilung des Wuchsstoffes bei Bäumen. Zeits. Bot. **30**: 209–252.

WOOD FIBER LENGTH AS RELATED TO POSITION IN TREE AND GROWTH

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INTRODUCTION

The size of tracheids in conifers and of fibers and vessel segments in dicots has been a subject of investigation for nearly 80 years. Foresters have been interested in woody cell size because of the real or assumed correlation between it and the strength properties of wood and paper, while botanists have been equally interested from the standpoint of its possible relation to evolution, growth and senescence. The present report is a review of the literature from the morphogenetic viewpoint. Special attention is given to the data published rather than to the conclusions previously drawn in an effort to assess the possible interrelationships between cell size of trees and developmental factors of growth and senescence. Because most of the available data apply to the tracheids of gymnosperms, emphasis will be placed on these, but data will be brought in on dicotyledons wherever possible.

THE WORK OF SANIO

Modern interest in the length of tracheids as related to position in the tree dates from Sanio (1872, 1873) who has been cited by practically every subsequent worker, although the frequent repetitions of errors in the citations indicate that many did not actually refer to his work. Sanio measured the tracheid length in Scotch pine (*Pinus sylvestris*) in various parts of the stem and branches. Since his conclusions have been dignified as laws by Bailey and Shepard (1915) and have formed the basis for much subsequent discussion, they are quoted as follows in English translation:

1. Tracheids in the stem and branches generally increase in size from the inside toward the outside through a number of annual rings, until a definite size is reached, which then remains constant for the following annual rings.

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2. The final size of the tracheids in the stem increases from the bottom toward the top; at a definite height it reaches a maximum and then decreases toward the crown.

3. The final size of the tracheids in the branches is less than in the stem but depends upon the latter in that those branches which arise at such a stem-height that the stem tracheids are larger, themselves have larger cells than do those branches which arise at a stem-height where the constant cell size is less.

4. Also in the branches the constant cell size increases in the outer rings towards the tip, and then again falls. In the irregular gnarled growth of the crown branches, cell size is irregular; thus I have observed in these branches for I have found throughout a considerable length, a double rising and falling. The normal growing branches of old bushy spruce probably follows a fixed and similar rule as in the neighboring stem, although I have not investigated this.

5. In the root the width of the cells first increases through the cross-sectional area, then falls, and then rises again until the constant size is reached. Also, toward the end of the root an increasing size is found, though I have not yet investigated this question with sufficient preciseness, due to the lack of suitable material.

The findings of Sanio have been reproduced in some detail because of the pioneer character of his investigations. At the same time it should be noted that many later studies are based on larger masses of data and take more important variables into account.

Since Sanio's initial efforts, a great deal of further work has been done, particularly in the United States, Canada and Australia. This may be classified into four groups: *a*) the effect of position within the stem on the length of wood fibers, *b*) the relationship between stem tissues and fiber length, *c*) fiber length in roots and branches, and *d*) correlations between tracheid length and growth factors.

POSITION WITHIN THE STEM

Most interest has centered on the effect of position within the stem on the length of wood fibers. Bailey and various associates have been particularly active in attacking this problem. In 1914 Shepard and Bailey (see also Bailey and Shepard, 1915) published the results of tracheid length determinations in basal sections of

white pine (*Pinus strobus*), white fir (*Abies concolor*), longleaf pine (*Pinus palustris*) and eastern hemlock (*Tsuga canadensis*). They found that the average fiber length increased outward from the center but fluctuated widely in the outer rings instead of remaining constant as suggested by Sanio. For one 50-year-old red spruce (*Picea rubra*), they studied sections from various heights in the stem and confirmed Sanio to the effect that tracheid length increased up to a given point and then decreased toward the top.

Similar studies were undertaken by Gerry (1915, 1916) with white pine, longleaf pine and Douglas-fir (*Pseudotsuga taxifolia*). She found that the fiber length increased outward from the pith at both the base and top of an 82-foot-tall, 250-year-old white pine, and that at a distance of two and one-half to three inches from the pith, the increase in fiber length was apparent for approximately two-thirds the height of the tree. In her second paper she found that the increase in tracheid length was marked during the first 20 years but that subsequent lengths were erratic and hardly constant.

Pritchard and Bailey (1916) extended the study to hardwoods by working with shagbark hickory (*Carya ovata*). They found that both the length of fibers and of vessel segments increased from the pith outward in a 60-year-old sprout, a 65-year-old seedling and a 255-year-old old-growth tree for at least the first 20 years, but that they remained nearly constant during the later stages of tree development. Fiber and vessel segment length also increased up the stem until a maximum was reached, and then decreased. The diameter of vessel segments, however, seemed to increase throughout the life of the old growth tree, being 0.06 mm at one year, 0.18 mm at ten years, 0.22 mm from 20 to 80 years, 0.26 mm from 80 to 160 years, and 0.33 mm from 160 to 255 years.

Lee and Smith (1916) studied fiber length in Douglas-fir from British Columbia and noted a rapid increase in length for the first 30 to 40 years before it slowed down. As successive annual rings were laid down, the longest fibers were formed at successively higher levels in the stem. Thus the longest fibers in the 30th annual ring averaged 3.52 mm and occurred ten feet from the ground; in the 70th ring they averaged 5.26 mm and occurred at 34 feet; in the 110th ring they averaged 6.07 mm and occurred at 42 feet; in the 150th ring they averaged 6.17 mm and occurred at 98 feet; and in the 190th ring they averaged 6.31 mm and still

occurred at 98 feet. The tree was 195 feet tall and had a clear length of 141 feet. It will be noted that the average length of the longest fibers increased with age but that such fibers occurred at different heights so that they could not be sampled with a single cross-section.

The first comprehensive summary of North American work appeared in 1919. Bailey and Tupper published tracheid length data for many species and summarized in graphical form the relation of tracheid length to annual ring (or age). Their data were drawn in part from previously cited work and in part were original. In addition to the species already listed, they presented tracheid length over age data for *Dioon spinulosum, Araucaria Bidwellia, Pinus ponderosa, Cedrus Libani, Taxus brevifolia, Pinus albicaulis* and others.

Bailey and Tupper explained the variation in fiber length within the stem as a function of the distance from the root or branches:

"In other words, it seems probable that as a plant becomes older, the depressing effect of the conditions at the base of a plant extends further and further up the stem, and persistent branches have a progressively greater influence upon the surrounding tissue of the main axis of the plants. Therefore, in certain sections removed from the bases and tops of large trees, it is not uncommon to find that the tracheary elements—after increasing in length for a period of years—tend to become shorter in the outermost rings of the stem; a phenomenon which might easily be mistaken for senility".

The above statement is discussed later. Bailey and Tupper's paper was followed in 1920 by a paper by Bailey in which tracheid size in the outermost growth layer of the xylem was related to the length of the cambial initial. It was found that the length of the initial was only slightly less than that of the tracheid corresponding. In other words, the size of the tracheid is determined largely by the size of the cambial initial in many species and only secondarily by changes that take place subsequently in the cell.

The work prior to 1920 has been confirmed in many later studies. Lee (1922) found similar trends in black (*Picea mariana*) and white spruce (*Picea glauca*) as did MacMillan for red spruce in 1925. Kribs (1928) provided precise data for jack pine (*Pinus banksiana*). Bailey and Faull (1934) published data from

redwood (*Sequoia sempervirens*). In a section of stump five feet in diameter from a 420-year-old tree, the tracheid length increased from 0 to 210 years, stayed constant from 210 to 380 years, and decreased from 380 to 410 years.

More recent workers (Myer, 1931; Berkeley, 1934; Siriban, 1939; Misra, 1939; Graff and Miller, 1939; Garland, 1939; Bannan, 1941, 1942, 1944; Bethel, 1941; Cortes and Hambananda, 1947; Liang, 1948) have tended to confine themselves to checking previous findings in their own material, to avoid excessive duplication and to concentrate upon related points.

Bisset (1949) has compiled a bibliography and summarized the data on the variations of tracheid and fiber lengths and their distribution in angiosperms and gymnosperms.

Bisset and Dadswell (1949) found that the fiber length of late wood varied throughout the tree from 0.6 mm in the ring next to the pith at all levels to 1.35 mm in the outermost rings at the 50-foot level in a 50-year-old, 172-foot-tall *Eucalyptus regnans*. There was a rapid increase in length of fibers from the center of the tree outwards for about ten growth rings, after which a more or less constant value was reached.

Hata (1949) came to the following conclusions concerning *Pinus densiflora*: *a*) tracheid length in cross-sections of stems and branches at first increases from the center outwards, reaches a maximum, and then remains constant; *b*) in a given growth ring, tracheid length first increases with the height in the tree, reaches a maximum, and then decreases; *c*) the length of tracheids in the annual ring nearest the pith increases with height up to 1.5 to 3 m above the ground and then remains constant or varies irregularly.

Abies concolor, A. procera and *Pseudotsuga taxifolia* were studied by Anderson (1951) who found a direct relationship between the length of tracheids and their distance from the pith. This relationship was independent of height, provided the cross-section was somewhat above the ground level, and could be stated in mathematical terms. At the two-foot level, however, the tracheid were definitely shorter than at greater heights, and this difference increased with increasing distance from the pith. *Fraxinus excelsior* was investigated by Bosshard (1951), and fiber length was found to increase outward from the pith in the first 30 annual rings and then to decrease in any cross-section.

Wardrop (1948) attributed the increased tracheid length in successive annual rings to the seasonal flow of growth hormones that accompanies the opening of buds and resumption of apical growth. By applying external radial pressure upon growing conifer stems, he demonstrated that shorter tracheids were formed. This he attributed to increased number of transverse divisions in the cambium. Shimaji (1950) examined fibers of *Cladrastis shikokiana, Platyosprion platycarpum, Fagus japonica* and *F. crenata,* and proposed that the tension on the cambium may be the limiting factor on the fiber length for at least part of the tree's life. Bosshard (1951) showed that the cambium initials themselves increased in length with increasing age, thus resulting in increased fiber length in successive annual rings of *Fraxinus excelsior.*

STEM TISSUES

Gerry (1916) reported that the early or springwood tracheids in *Pinus palustris* and *Pseudotsuga taxifolia* are in general longer than the late or summerwood tracheids. On the other hand, Chalk (1930) found that summerwood tracheids average 12 per cent longer than those of springwood in *Picea sitchensis.* Kribs (1928) also noted that late wood tracheids (in *Pinus banksiana*) are somewhat longer than those in the early wood in most cases.

Investigations made by the Australian Division of Forest Products (1949) showed that considerable variation exists in fiber length within one growth ring of *Eucalyptus gigantea* and other eucalypts with prominent growth rings. The shortest fibers were found in the first-formed early wood; the longest, about 50 per cent longer, in the last-formed late wood. Hardwoods from different parts of the world were used to show that in all hardwoods with definite growth rings, considerable variation in any one growth ring as to fiber length could be expected. In tropical hardwoods, on the other hand, no great variation in fiber length occurred. Preliminary work on coniferous timbers suggested late wood tracheids to be slightly, but significantly, longer than early wood tracheids. Bisset and Dadswell (1949) found in one tree of *Eucalyptus regnans* that the last-formed late wood fibers were consistently longer than those of the early wood. Bisset, Dadswell and Amos (1950) confirmed the earlier findings of the Australian Division of Forest Products (1949). Among the gymnosperms

examined were *Pseudotsuga taxifolia, Picea sitchensis, Pinus banksiana* and *P. radiata.* Late wood tracheids were in all instances slightly longer (up to 11 per cent) than the early wood tracheids.

Bosshard (1951) detected late wood fibers in *Fraxinus excelsior* up to 79 per cent longer than the early wood fibers. Vasiljevic (1952) divided the growth ring into five equal parts and numbered them from one to five from within towards the bark. Cells in 1 were shorter than in 5 for *Cornus mas, Ailanthus altissima* and *Morus alba*; 1 longer than 5 for *Tilia tomentosa* and *Prunus domestica*; 1 equal to 5 for *Corylus avellana.* The maximum cell length occurred in 2–3 for *Tilia,* 2–4 for *Prunus* and *Ailanthus,* 3 for *Morus,* 3–4 for *Corylus* and *Cornus.*

Compression wood fibers seem invariably shorter than those of normal wood. This has been demonstrated for *Pinus radiata, P. pinaster, Picea sitchensis* and *Pseudotsuga taxifolia,* among other species (Lee and Smith, 1916; Aust. Div. For. Prod., 1949; Bisset and Dadswell, 1950; Wardrop and Dadswell, 1950, 1952).

A number of investigators, among them Harlow (1927) and Graff and Miller (1939), have demonstrated that there is a close linear correlation between average tracheid diameter and average tracheid length, and that each measurement may be used in tracheid size studies involving gymnosperms.

BRANCHES AND ROOTS

Many similar studies have been made on tracheid length in branches and roots. Sanio (1872) had found that tracheids in branches of *Pinus sylvestris* were shorter than those in the stem, but that they were similar in that their size increased from the pith outwards and from the base of the branch outwards for a certain distance. Baranetzky (1901) confirmed these findings and demonstrated, in addition, that the average length of the tracheids on the upper side of the branch in each annual ring, except the first, was greater than on the lower side where compression wood was formed. The closer the angle of the branch approached the horizontal, the greater was the difference. This relation held for *Pinus sylvestris, Larix europea, Aesculus hippocastanum* and *Tilia.* By fixing the morphologically lower side in the physically upper position, he determined that the length of the tracheids was geotropi-

cally controlled. Hata (1949) observed that tracheid lengths in *Pinus densiflora* were longer in the stem than in the branches and longer in thick branches than in thin branches.

Tracheid length from the pith outward in the stem, branches and roots of *Sequoia sempervirens* were studied by Bailey and Faull (1934). The longest tracheids were found in the roots, the shortest in the branch. On the other hand, Fegel (1941) noted that both vessel segments and wood fibers in a variety of ring-porous and diffuse-porous hardwoods tended to be slightly shorter in the roots than in the trunk. In *Pinus strobus* and *P. resinosa* the root tracheids were longer than the trunk tracheids, but in six other conifers (*Picea rubra, P. mariana, Larix laricina, Tsuga canadensis, Abies balsamea, Thuja occidentalis*) the root tracheids averaged only 2.11 mm. while those in the stem averaged 3.53 mm. In all cases—ring-porous hardwoods, diffuse-porous hardwoods, conifers—branch fibers were shorter than those in the roots and trunks.

GROWTH CORRELATIONS

Finally, in the survey of previous work on fiber length, there remains the problem of the relation of growth to cell size. Much has been done on this, but few investigators have concentrated upon the subject, and the findings are to some extent contradictory and inconclusive.

Mell (1910) studied fiber length in California walnut (*Juglans californica*) growing on three sites. He made his measurements three to four rings inside the bark so that age was held constant, and found that trees growing on the best site, a deep black soil, had longer fibers (1.13 mm) than those growing on moderately moist soil (1.01 mm) or those growing on dry sand and gravel (0.97 mm). The above values refer to average fiber length, but similarly consistent results were obtained when maximum fiber length and minimum fiber length were used.

On the other hand, several investigators have been unable to find any close correlation between width of growth ring and fiber length (Shepard and Bailey, 1914; Bailey and Shepard, 1915; Gerry, 1916; Lee and Smith, 1916; Berkley, 1934). In these studies, relatively few data dealing with growth correlations were available.

In contrast, an increasing number of workers have been finding at least some relation between tracheid or fiber size and growth rate. Lee and Smith (1916), although failing to find any demonstrable relation between tracheid length and the rate of diameter increment, did conclude that the faster the height growth, the longer were the fibers. Lee (1917) found that a very fast-grown white spruce (*Picea glauca*) had tracheids approximately ten per cent longer than those of normally grown trees. Bailey and Tupper (1919) concluded that short tracheids are characteristically found in " xerophytes, small, slowly-growing or depauperate individuals, and plants whose stems are clothed nearly to the level of the ground with large persistent branches ". They did, however, attribute this feature to branch and root habit instead of growth rate.

MacMillan (1925) found that for red spruce (*Picea rubra*) the tracheids laid down in free-growing trees were at every age longer than those laid down in suppressed trees, the average length of the former being 2.52 mm and of the latter, 2.79 mm. Harlow (1927) found that the rate of increase in tracheid length in northern white cedar (*Thuja occidentalis*) growing on limestone (good site) was greater with increasing age than that of trees growing in peat (poor site). Ninety-year-old trees on the limestone site had tracheids in their outer growth rings slightly larger than those of 160-year-old trees on the peat site.

Berkeley (1934) noted that for trees of the same species of southern pine of the same age and growth rate, the tracheid length was approximately the same for a given position in the tree, but that, other factors being equal, growth rate affected tracheid length. Several far eastern investigators (Siriban, 1939; Misra, 1939; Cortes and Hambananda, 1947) have reported that for several native species, the longest wood fibers are found in the larger and faster-growing trees.

Bannan (1941, 1942, 1944) reported that for northern white cedar (*Thuja occidentalis*) in Ontario, the longest root tracheids were in the sand where root growth was greatest, and the shortest root tracheids in swampy soils where root growth was restricted. Furthermore, when the soil had been stripped from the roots, subsequent tracheids laid down were stem-like in character and shorter than those characteristic of the roots. In eastern red cedar (*Juni-*

perus virginiana) the largest root cells were found in more or less uniform soil, while in roots wedged between stones, the tracheids were small and thick-walled with late wood sometimes constituting a large proportion of the growth rings.

Liang (1948) investigated the variation in tracheid length one foot from the ground in one stem of each of three larches (*Larix decidua, L. leptolepis, L. eurolepis*). Tracheid length was related at a highly significant level to growth per cent as indicated by the ratio of (*a*) the distance from the pith to the outer edge of a given growth ring to (*b*) the distance from the pith to the outer edge of the growth ring laid down two years earlier. Although age was found to be significantly related to tracheid length when considered independently, it had no significance when the effect of growth per cent was held constant.

Hata (1949) found that tracheid length of *Pinus densiflora* varied inversely with annual-ring breadth and that the tracheids were longer in fast- than in slow-growing trees. Amos, Bisset and Dadswell (1950) confirmed the earlier results of the Australian Division of Forest Products (1949) that the shortest, widest fibers were laid down at the period of maximum growth, while the longest, narrowest ones were produced at the period of minimum growth in *Eucalyptus gigantea.*

Bisset, Dadswell and Wardrop (1951) investigated tracheid length variation in *Pinus radiata* and *P. pinaster.* For them wider growth rings had lower average tracheid lengths than narrow rings. There was some evidence of similar correlation between stems. Trees with a high initial tracheid length maintained this relatively high length throughout subsequent growth rings. Different "strains" of *Pinus pinaster* had different initial tracheid lengths.

DISCUSSION

A consideration of the work that has been done on fiber length leads one to believe that both position in tree and growth characteristics are related factors.

First, as to position in tree, it is necessary to distinguish between analyses in which age is counted from the center outward and those in which the rings are counted from the outside in. In the former case the age of the ring is not considered but only the time that has elapsed since formation of the pith at that point in

the tree. In the latter case the age of the ring is known but not its relation to pith formation.

For any given cross-section it is apparent that the first tracheids or other wood fibers laid down in the first annual ring are very short. The second ring fibers are notably longer. In each successive ring the fibers average somewhat longer until, after 20 to 50 years, they reach a maximum length. In subsequent years the fibers remain about the same length, although they may vary considerably about the mean size. Finally in some sections a noticeable decrease in fiber length is noted in the outer rings.

Comparing various cross-sections, it is apparent that fiber length is more related to the position of the ring with regard to the pith than to the age at which the ring is laid down. Krib's data illustrate this well. The tenth ring counted out from the pith has at all heights about a half-millimeter longer tracheids than does the fifth annual ring counted out from the pith.

Nevertheless, the age of the annual ring also affects fiber length. When the data of Shepard and Bailey (1914) and of Pritchard and Bailey (1916) are arranged on this basis, they illustrate the fact that the tracheids in each successive annual ring average larger than those in the preceding ring, although the longest fibers in any given ring do not occur in the same cross-section. Instead, the longest fibers in the later-formed rings occur higher up the stem than in the earlier-formed rings.

Considering the above factors and also the data noted for tracheid and wood fiber length in branches and roots, it is apparent that position in the tree has a major effect upon the length of fibers. A single cross-section can not be expected to yield finite results, as the fibers in the outer portion of the section occupy a different relative position (i.e., farther from the longest fibers) in their growth ring than do those in the inner portion. In order to assess the influence of growth factors on fiber length, therefore, it is advisable to study a series of cross-sections up the stem and to take into account the effect of position on fiber length. When this is done it is apparent that growth in some form is closely related to fiber length. The trend in fiber length in successive annual layers of wood tends to follow the normal growth curve of the tree. Fibers are short at first. In early years, when the tree is growing fast, the fibers lengthen out quite rapidly. Throughout

maturity, when the tree is growing steadily, fiber length remains at about the same average value. Finally, in very old trees fiber length apparently decreases as does growth.

The profound influence of growth upon fiber length, once position in tree has been taken into account, is indicated not only by the internal evidence within a single tree but also by the studies relating fiber length between trees of different growth rates, growing on different sites, etc.

Yet, the problem is still complicated. Granted that rapid growth leads to long fibers—or is related to long fibers, for the cause and effect relationship is scarcely understood—there still remains the question of what measurement of growth should be taken. Diameter growth seems to be an inadequate measure. Height growth is much more promising, although practically no direct evidence of the relation of height growth to fiber length is available. Quite probably, the significant growth is that related to the amount or speed of photosynthesis or root absorption. The question remains to be studied.

We are then confronted with a mass of data that demonstrates certain relationships between cell size in woody plants and both position in the tree and growth in some sense. The descriptive material is good. Adequate explanations remain to be made and must await the experimental correlation of anatomical characteristics with physiological, genetic and ecological factors. The explanation of Bailey and Tupper (1919) that fiber length is governed by the retarding effect of roots and stems really does not explain anything, does not hold in many cases, and in any event is patently too simple to suffice. Woody cell size (or size of the cambial initials if you will) is clearly a function of both organization and growth. Further, the study of wood fiber size seems to indicate the possibility of senescence in older trees, although it does not offer any evidence as to whether such senescence is genetic, physiological or environmental in origin.

Finally, the problem of relating growth to fiber length can not be completely segregated from the larger problem of relating growth to other anatomical characteristics of wood. The same growth and structural factors that affect fiber length also exert an effect on the type of tissue produced, the amount of reaction wood and other anomalies produced, and on the specific gravity of the

resulting wood mass. Surveys of the effect of growth rate on specific gravity in conifers (Spurr and Hsiung, 1954) and on compression wood in conifers as a morphogenetic phenomenon (Spurr and Hyvärinen, 1954) should be read in connection with the present discussion.

BIBLIOGRAPHY

AMOS, G. L., I. J. W. BISSET and H. E. DADSWELL. 1950. Wood structure in relation to growth in *Eucalyptus gigantea* Hook F. Aust. Jour. Sci. Res. **3B**: 393–413.

ANDERSON, ERIC A. 1951. Tracheid length variation in conifers as related to distance from pith. Jour. For. **49**: 38–42.

Australia Division of Forest Products. 1949. Cell wall and fibre studies. Growth studies. Sapwood and heartwood. Rep. Div. For. Prod. Aust. 1948–1949: 6–10. [Not seen. Abstracted in For. Abs. **11**: 1852.]

BAILEY, I. W., and H. B. SHEPARD. 1915. Sanio's laws for the variation in size of coniferous tracheids. Bot. Gaz. **60**: 66–71.

———— and W. W. TUPPER. 1919. Size variation in tracheary cells. Proc. Am. Acad. Arts & Sci. **54**: 149–204.

————. 1920. The cambium and its derivative tissues. II. Size variations of cambial initials in gymnosperms and angiosperms. Am. Jour. Bot. **7**: 355–367.

———— and ANNA F. FAULL. 1934. The cambium and its derivative tissues. IX. Structural variability in the redwood, *Sequoia sempervirens*, and its significance in the identification of fossil woods. Jour. Arn. Arb. **15**: 233–254.

BANNAN, M. W. 1941. Wood structure of *Thuja occidentalis*. Bot. Gaz. **103**: 295–309.

————. 1942. Wood structure of the native Ontario species of *Juniperus*. Am. Jour. Bot. **29**: 245–252.

————. 1944. Wood structure of *Libocedrus decurrens*. Am. Jour. Bot. **31**: 346–351.

BARANETZKY, J. 1901. Ueber die Ursachen, welche die Richtung der Aeste der Baum- und Straucharten bedingen. Flora **89**: 138–239.

BERKLEY, E. E. 1934. Certain physical and structural properties of three species of southern yellow pine correlated with the compression strength of their wood. Ann. Mo. Bot. Gard. **21**: 241–338.

BETHEL, J. S. 1941. The effect of position within the bole upon fiber length of loblolly pine (*Pinus Taeda* L.). Jour. Four. **39**: 30–33.

BISSET, I. J. W. 1949. I. Bibliography of references on the variations of tracheid and fiber lengths and their distributions in angiosperms and gymnosperms. II. Summarized data on the variation of fibre and tracheid lengths and their distribution in angiosperms and gymnosperms. Bibliogr. Ser. Div. For. Prod. Aust. **37**. 5 + 5 pp. [Not seen].

———— and H. E. DADSWELL. 1949. The variation of fibre length within one tree of *Eucalyptus regnans* F. v. M. Aust. For. **13**: 86–96.

————, ———— and G. L. AMOS. 1950. Changes in fibre-length within one growth ring of certain angiosperms. Nature [London] **165**: 348–349.

———— and ————. 1950. The variation in cell length within one growth ring in certain angiosperms and gymnosperms. Aust. For. **14**: 17–29.

————, ————, and A. B. WARDROP. 1951. Factors influencing tracheid length in conifers stems. Aust. For. **15**: 17–30.

BOSSHARD, H. H. 1951. Variabilität der Elemente des Eschenholzes in Funktion von der Kambiumtätigkeit. Schweiz. Z. Forstw. **102**: 648–665.

CHALK, L. 1930. Tracheid length, with special reference to Sitka spruce (*Picea sitchensis* Carr.). Forestry **4**: 7–14.

CORTES, R. T., and P. HAMBANANDA. 1947. Fiber length of anilau (*Columbia serratifolia*), hinlaumo (*Mallotus ricinioides*) and kupang (*Parkia javanica*). Phil. Jour. For. **5**(1) : 50–70.

FEGEL, A. C. 1941. Comparative anatomy and varying physical properties of trunk, branch and root wood in certain northeastern trees. N. Y. State Coll. For., Tech. Bul. **55**. 20 pp.

GARLAND, H. 1939. A microscopic study of coniferous wood in relation to its strength properties. Ann. Mo. Bot. Gard. **26**: 1–94.

GERRY, ELOISE. 1915. Fiber measurement studies; length variations: Where they occur and their relation to the strength and uses of wood. Science **41**(1048) : 179.

————. 1916. A comparison of tracheid dimensions in longleaf pine and Douglas fir, with data on the strength and length, mean diameter and thickness of wall of the tracheids. Science **43**(1106) : 360.

GRAFF, J. H., and R. W. MILLER. 1939. Fiber dimensions. Paper Trade Jour. **109**(6) : 31–37.

HALE, J. D. 1924. Effect of rate of growth on density and fibre characteristics of pulpwood. Pulp & Paper Mag. Canada **43**. March 6, 1924.

———— and FENSOM, K. G. 1931. The rate of growth and density of the wood of white spruce. Canada Dept. Int. For. Serv., Circ. 30. 16 pp.

————. 1935. The structure of wood. *In:* T. A. McElhanney et al: Canadian Woods. Their properties and uses. Pp. 101-132.

HARLOW, W. M. 1927. The effect of site on the structure and growth of white cedar, *Thuja occidentalis* L. Ecology **8**: 453–470.

HATA, K. 1949. Studies on the pulp of Akamatsu (*Pinus densiflora* Sieb. et. Zucc). I. On the length, diameter and length–diameter ratio of tracheids in Akamatsu wood. Kawaga-Ken Agr. Coll., Tech. Bull. **1**: 1–35. [Not seen. Abstracted in For. Abs. **14**: 629].

KRIBS, D. A. 1928. Length of tracheids in jack pine in relation to their position in the vertical and horizontal axis of the tree. Minn. Agr. Exp. Sta., Bul. 54. 14 pp.

LEE, H. N. 1917. Fast-growing white spruce in Quebec. Canad. For. Jour. **13**: 1439–1440.

————. 1922. The manufacture of pulp and paper. Vol. 3, Sect. 1. Properties of pulpwood, pp. 1–39. 1922.

———— and E. M. SMITH. 1916. Douglas fir fiber with special reference to length. For. Quart. **14**(4) : 671–695.

LIANG, SHIH-CHEN. 1948. Variation in tracheid length from the pith outwards in the wood of the genus *Larix* with a note on variation in other anatomical features. Forestry **22**: 222–237.

MACMILLAN, W. B. 1925. A study in comparative lengths of tracheids of red spruce grown under free and suppressed conditions. Jour. For. **23**: 34–42.

MCELHANNEY, T. A. 1935. Canadian woods. Their properties and uses. Chap. II. Commercial timbers of Canada, pp. 28–100.

MELL, C. D. 1910. Determination of quality of locality by fiber length of wood. For. Quart. **8**: 419–422.

MISRA, P. 1939. Observations on spiral grain in the wood of *Pinus longifolia*. Forestry **13**: 118–133.

MYER, J. E. 1930. The structure and strength of four North American Woods as influenced by range, habitat, and position in the tree. N. Y. State Col. For., Tech. Publ. 31. 39 pp.

PRITCHARD, R. P., and I. W. BAILEY. 1916. The significance of certain variations in the anatomical structure of wood. For. Quart. **14**(4) : 662–672.

SANIO, K. 1872. Ueber die Grösse der Holzzellen bei der gemeinen Kiefer (*Pinus sylvestris*). Jahrb. Wiss. Bot. **8**: 401–420.

SHEPARD, H. B., and I. W. BAILEY. 1914. Some observations on the variation in length of coniferous fibers. Proc. Soc. Am. For. **9**: 522–525.

SHIMAJI, K. 1950. The relation between fibre length of some dicotyledonous woods and tension on the cambium. Jour. Jap. For. Soc. **32**: 371–372. [Not seen. Abstracted in For. Abs. **14**: 1495].

SIRIBAN, F. L. 1939. Fiber measurement studies of anabiong. Phil. Jour. For. **2**: 301–313.

SPURR, S. H., and W. Y. HSIUNG. 1954. Growth rate and specific gravity in conifers. Jour. For. **52**: 191–200.

———— and M. HYVÄRINEN. 1954. Compression wood in conifers as a morphogenetic phenomenon. Bot. Rev. **20**: 551–560.

VASILJEVIĆ, S. 1952. O dužini mehaničkih elemtata u granicama prstena prirasta. [Length of mechanical elements within the growth ring]. Glasn. šum. Fak., Beograd **5**: 257–264. [Not seen. Abstracted in For. Abs. **14**: 2609].

WARDROP, A. B. 1948. The influence of pressure on the cell wall organisation of conifer tracheids. Proc. Leeds Phil. Lit. Soc. **5**: 128–135.

———— and H. E. DADSWELL. 1950. The nature of reaction wood. II. The cell wall organization of compression wood tracheids. Aust. Jour. Sci. Res. **B. 3**: 1–13.

———— and ————. 1952. The nature of reaction wood. III. Cell division and cell-wall formation in conifer stems. Aust. Jour. Sci. Res. **B. 5**: 385–398.

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